PLANT RESISTANCE

Improved Dry-Fleshed Sweetpotato Genotypes Resistant to Insect Pests

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ABSTRACT Thirty-five mostly dry-fleshed sweetpotato, Ipomoea batatas (L.) Lam. (Convolvulaceae), genotypes from the USDA-ARS/Clemson University sweetpotato breeding program were evaluated in nine field experiments at the U.S. Vegetable Laboratory, Charleston, SC, from 1998 to 2004. There were highly significant entry effects for percentage of uninjured roots; wireworm, Diabrotica, and Systena (WDS) index; percentage of roots damaged by sweetpotato weevil, Cylas formicarius elegantulus (Summers); percentage of roots damaged by sweetpotato flea beetle, Chaetocnema confinis Crotch); and percentage of roots damaged by white grub larvae (primarily Plectris aliena Chapin). The susceptible control, 'SC1149-19', had a significantly lower percentage of uninjured roots, a significantly higher WDS rating, and higher percentage infestations of flea beetle, grubs, and sweetpotato weevils than all other sweetpotato entries in this study. Twenty-seven genotypes had significantly less insect damage than 'Beauregard', the leading commercial orange-fleshed cultivar in the United States. In addition, 11 genotypes had significantly less insect injury than 'Picadito', a commercial boniato-type sweetpotato grown extensively in southern Florida. Overall, no genotypes were more resistant to soil insect pests than the resistant checks 'Sumor' and 'Regal'. Many of the advanced dry-flesh sweetpotato genotypes had high levels of resistance to soil insect pests, and they represent a useful source of advanced germplasm for use in sweetpotato breeding programs.

KEY WORDS plant resistance, *Ipomoea*, *Diabrotica*, *Cylas*, white grub

Sweetpotato, Ipomoea batatas (L.) Lam. (Convolvulaceae), is one of the world's most important food crops, especially in developing countries (Woolfe 1992). Tropical, dry-fleshed sweetpotatoes are a major source of sustenance in much of Asia, Oceania, the Caribbean, Latin America, and Sub-Saharan Africa, and this crop is widely grown as a security food crop that is crucial for efforts to solve world hunger (CIP) 2004). Although Asia and Africa produce ≈95% of the world's sweetpotatoes (Huaccho and Hijmans 2000), this crop is also important in the United States, Latin America, and the Caribbean nations (Horton 1988). Most consumers in the United States prefer sweetpotatoes with dark copper skin and sweet, moist-orange flesh. However, in Africa, Asia, and the Caribbean, consumers prefer cream or white-fleshed sweetpotatoes that have low sweetness and a dry texture (Martin and Rodriguez-Sosa 1985).

In the United States, dry-fleshed sweetpotatoes are sold in markets that cater to ethnic Caribbean, Latin American, African, and Asian communities, which

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consume disproportionately more sweetpotatoes than other segments of the U.S. population (Gull and Conover 1977). These white, dry-fleshed types are known as boniatos (or Cuban sweetpotatoes) in Hispanic communities (O'Hair et al. 1983). In the United States, most dry-fleshed sweetpotatoes are grown in Florida, California, Hawaii, and Puerto Rico (Martin 1983, 1987; O'Hair et al. 1983; Valenzuela et al. 1994; May and Scheuerman 1998); however, other states recently have become interested in growing dryfleshed types.

Throughout the world, production of sweetpotatoes is severely limited by several insect pests, and improved pest management approaches for this crop are needed (Schalk et al. 1991, Talekar 1991, Lawrence et al. 1997, Jackson et al. 2002). The primary soil insect pests of sweetpotato in the United States are spotted cucumber beetle, Diabrotica undecimpunctata howardi Barber; banded cucumber beetle, Diabrotica balteata LeConte; sweetpotato flea beetle, (Chaetocnema confinis Crotch; elongate flea beetle (Systena elongata (F.); wireworm larvae (Conoderus spp.); white grub larvae (Phyllophaga spp. and Plectris aliena Chapin); and sweetpotato weevil, Cylas formicarius elegantulus (Summers) (Cuthbert 1967). Among these pests, the sweetpotato weevil is the most important worldwide (Jansson and Raman 1991).

Historically, management of sweetpotato insect pests has relied on chemical insecticides and cultural

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practices. However, control of insects with insecticides can be expensive and unreliable, and it may cause environmental or safety concerns. In some instances, insecticides fail to provide adequate protection to roots, and yield losses due to insects can exceed 50%, especially in countries where low-input agricultural systems predominate (Lawrence et al. 1997). Effective, low-input, environmentally benign integrated pest management (IPM) approaches are needed as alternatives to chemical pest control (Schalk et al. 1993, Lawrence et al. 1997).

Host plant resistance is an attractive approach that fits well into sweetpotato IPM programs (Collins et al. 1991, Lawrence et al. 1997). The usefulness of insect-resistant sweetpotato cultivars in IPM programs has been well demonstrated (Cuthbert and Jones 1978, Jones et al. 1987). The incorporation of breeding lines in current sweetpotato pest management programs may be a practical and economical approach for managing pests in both low-input and high-intensive production systems throughout the world (Talekar 1991, Smit 1997, Alcázar et al. 1997, Jackson et al. 2002).

Various attempts at breeding for resistance in sweetpotatoes have been made (for reviews, see Jones et al. 1986; Collins et al. 1991; Schalk et al. 1991). Cockerham and Deen (1947) initiated a screening program to evaluate sweetpotato varieties for resistance to the sweetpotato weevil, and they first proposed that cultivars resistant to insect pests could be developed through a breeding program. Through a recurrent mass selection technique (Jones et al. 1986), the USDA-ARS, U.S. Vegetable Laboratory (USVL), Charleston Co., SC, in cooperation with Clemson University (Clemson, SC), has developed many breeding lines and cultivars with multiple pest resistance to diseases, nematodes, and insects including wireworms, Diabrotica spp., flea beetles, and white grubs (for review, see Schalk and Rolston 1992). This program, which emphasizes the development of resistant sweetpotato cultivars with good horticultural qualities, has operated continuously at the USVL since 1961 (Cuthbert and Davis 1970, Schalk and Rolston 1992). Moderate levels of resistance to the sweetpotato weevil also have been identified in the genotypes released from this program (Rolston et al. 1979, Mullen et al. 1981, Thompson et al. 1999).

Antibiosis, nonpreference (antixenosis), and tolerance are all important mechanisms in pest resistance of sweetpotatoes (Barlow and Rolston 1981, Mullen et al. 1981). The importance of volatile attractants, and feeding and oviposition stimulants to pest resistance was reviewed by Nottingham and Kays (2002). Antibiosis factors from the periderm and cortex of insectresistant genotypes also have been identified (Cuthbert and Davis 1971, Schalk et al. 1986, Peterson et al. 1998, Harrison et al. 2003).

The association between insect damage and soil depth of roots is well known (Burdeos and Gapasin 1980). Stathers et al. (2003) associated depth of roots, degree of soil cracking, and amount of foliage with degree of pest resistance of sweetpotato genotypes in Uganda. Sutherland (1986) stated that certain less-

susceptible varieties in India have thin tubers scattered within the ground well below the soil surface, whereas Pillai and Kamlam (1977) reported that deeprooting sweetpotatoes with a long "neck" are less susceptible to weevil attack. Talekar (1997) reported that cultivars with thin, woody stems received less damage from weevils than those with fleshy crowns. Early maturing varieties also generally have less insect damage than later maturing genotypes (Collins et al. 1991, Alcázar et al. 1997). These pseudoresistance factors that allow the roots to escape insect damage also can be exploited in IPM programs (Smit 1997).

Sweetpotatoes are a major source of vitamin A (as β -carotene), and ≈ 100 g of an orange-fleshed cultivar fulfill daily retinol requirements (Woolfe 1992). Unfortunately, most dry-fleshed cultivars are white or cream colored and do not provide the minimum daily requirements of vitamin A (Hagenimana et al. 1999). However, β -carotene itself is not responsible for the strong flavor usually associated with orange-flesh sweetpotatoes, and recently some cream or yellowfleshed breeding lines with higher β -carotene levels have been developed (Hagenimana et al. 1999). Dryfleshed cultivars are also of interest for use in sweetpotato chips, fries, flour, and other value-added products (Woolfe 1992). Sweetpotatoes with β -carotene, fiber, and complex carbohydrates produce more nutritious chips and fries than do white potatoes, Solanum tuberosum L (Solanaceae) (Woolfe 1992). We believe it is possible to develop insect-resistant, dryfleshed sweetpotato cultivars that possess the agronomic, nutritional, and culinary characteristics required for widespread acceptance. The objective of the research described herein was to evaluate insectresistant sweetpotato genotypes that could be used in the breeding program for the development and release of nutritious, dry-flesh cultivars.

Materials and Methods

The sweetpotato genotypes evaluated in this study were from the USDA-ARS/Clemson University sweetpotato breeding program and were developed using mass selection techniques (Jones et al. 1986). This procedure has been used successfully at the USVL for breeding for resistance to several soilborne diseases and insect pests found in the soil (Schalk and Rolston 1992). This ongoing program (Jones et al. 1986) uses a polycross nursery, which includes insectresistant parents, for the production of sweetpotato seeds. For this program, first-year seedlings are screened for nematode and disease resistance in the greenhouse and then evaluated in five-plant plots in the field for yield, quality, and pest resistance. Roots from first-year seedlings showing acceptable agronomic characteristics and insect resistance are carried forward in the breeding program to intermediate and then to advanced testing in the field (Jones et al. 1986, Schalk et al. 1991). The field evaluations of pest resistance have been done primarily at the USVL, where high populations of soil insect pests are found consistently (Cuthbert and Jones 1972).

Thirty-five sweetpotato entries, consisting of 11 control cultivars and 24 experimental dry-fleshed sweetpotato genotypes were evaluated in this study. Control genotypes included eight dry-fleshed cultivars: 'GA90-16' (PI 612703) (Kays et al. 2001, USDA 2005), 'HiDry' (PI 566633) (Hamilton et al. 1985, USDA 2005), 'Liberty' (developed as W-341) (Bohac et al. 2003), 'Picadito' (PI 634399) (O'Hair et al. 1983, USDA 2005), 'Sumor' (PI 566657) (Dukes et al. 1987, USDA 2005), 'Tanzania' (PI 595887) (Mwanga et al. 2001, USDA 2005), 'Tinian' (PI 153655) (USDA 2005), and 'White Regal' (Bohac et al. 2001). Also included were three moist orange-fleshed genotypes: 'Beauregard' (PI 566613) (Rolston et al. 1987, USDA 2005), 'SC1149-19' (PI 63440) (USDA 2005), and 'Regal' (PI 566650) (Jones et al. 1985, USDA 2005). Beauregard, SC1149-19, and Tanzania were insect-susceptible controls, whereas Liberty, Regal, Sumor, and White Regal were insect-resistant controls.

The sweetpotato genotypes were evaluated in nine replicated field trials at the USVL between 1998 and 2004. A single field trial was planted in 1998, 1999, 2000, 2003, and 2004, whereas two field trials were grown in 2001 and 2002. The planting dates for these experiments ranged from 23 June to 6 August. Each sweetpotato entry was planted in two to four replications of single row, 10-plant plots arranged in a randomized complete block experimental design. Trials consisted of 14–53 entries (average of 32 entries per test). Entries that were not included in at least three of the nine trials were dropped from further evaluation. Local production practices were followed, except that no insecticides were applied. When rainfall was not adequate during the growing season, supplemental irrigation was applied. Plots were harvested 116–147 d after planting with harvest dates ranging from 24 October to 11 December. Harvested roots were cured for ≈7 d at 35°C and 95% RH. After curing, storage rooms were cooled, and sweetpotatoes were held at ≈13°C and 90% RH. The total weight and number of roots in each plot were determined after the sweetpotatoes had been cured and immediately before they were evaluated for resistance to insects.

All individual storage roots were scored for insect damage by using previously published procedures (Schalk et al. 1991; Jackson et al. 1999, 2002). Among the parameters calculated was the severity index for the Wireworm, Diabrotica, and Systena (WDS) index (Cuthbert and Davis 1971), which was calculated by averaging the rating given to each root (1, 1-5) holes or scars; 2, = 6-10 holes or scars; and 4, >10 holes or scars). Injury by white grubs, sweetpotato flea beetles, and sweetpotato weevils were the percentages of total roots that showed any damage by these insects. The percentage of uninjured roots (undamaged by any of the soil insect pests) also was determined. Data from individual trials were combined for the 35 sweetpotato genotypes in this study. Because there were significant fluctuations in the levels of insect pest injury each year, data for individual parameters were weighted by multiplying each data point by a weighting factor calculated as a proportion of the average for that factor for that year against the average of that factor over all years. These data were then subjected to analysis of variance (ANOVA), and means were separated by Fisher least significant difference (LSD) at the 5% probability level for type I errors (PROC GLM, SAS Institute 1989).

Results and Discussion

Many dry-fleshed experimental genotypes in this study exhibited significant levels of resistance to soil insect pests (Table 1). The ANOVA indicated that there were highly significant differences for entry effects for WDS index, percentage of uninjured roots, percentage of sweetpotato flea beetle infestations, percentage of sweetpotato weevil infestations, and percentage of white grub infestations. There were no significant replication effects for any of the parameters. Overall, none of the experimental sweetpotato genotypes were more resistant to soil insect pests than were the resistant checks Sumor and Regal (Table 1), but four genotypes had a significantly higher percentage of uninjured roots than did White Regal, a whitefleshed, pest-resistant cultivar from the USDA-ARS/ Clemson University sweetpotato breeding program (Bohac et al. 2001).

SC1149-19, which has been used frequently as a susceptible control in field evaluations of sweetpotato germplasm (Jones et al. 1987; Rolston et al. 1979; Schalk et al. 1986, 1993; Jackson et al. 2002, 2003), was the most susceptible genotype in our study. This cultivar had a significantly lower percentage of uninjured roots than all other sweetpotato entries in this study (Table 1). Also, all other genotypes had a significantly lower WDS rating, and lower infestation percentages for flea beetles, grubs, and sweetpotato weevils than did SC1149-19 (Table 1).

Eleven genotypes had significantly less damage than Picadito (or 'Picadita'), a scarlet-skin, white-fleshed genotype imported from Cuba that makes up \approx 90% of the acreage of boniato-type sweetpotatoes in southern Florida (O'Hair et al. 1983, Lamberts and Olson 2004) (Table 1). Twenty-seven genotypes had significantly less insect damage than did Beauregard, the most widely grown, orange-fleshed sweetpotato cultivar in the United States. All but two genotypes had a significantly lower WDS rating than Beauregard, and nine genotypes had a lower WDS rating than Picadito.

Sweetpotato weevil infestations were light on most entries, and only four genotypes (W-364, 97-081, SC1149-19, and Beauregard) had significantly higher weevil infestations than did the moderately resistant controls, Regal and Sumor (Table 1). These four genotypes also had significantly higher weevil infestations than did Picadito, which is consistent with a report by Waddill and Conover (1978) that this variety was less susceptible to sweetpotato weevil infestations than other commercial white-fleshed varieties in southern Florida.

The ANOVA indicated that there were highly significant differences for entry effects for total plot weight. Average yields (weight per plot) varied con-

Table 1. Average insect damage ratings and yields for 35 sweetpotato genotypes grown in replicated field plots from nine field trials at Charleston, SC, 1998–2004 (sweetpotato genotypes ranked by percent uninjured roots)

Sweetpotato ^a genotype	% uninjured roots	WDS^b index	% flea beetle ^c infestation	% grub ^d infestation	% weevil ^e infestation	Avg wt/plot(kg)	No. plots evaluated
W-326	76.5a	0.170n	3.8k-m	8.3c-k	1.4ef	1.3m-q	10
W-390 (94-145)	76.4a	0.203n	4.3j-m	1.3lmc	0.4f	2.5h-l	26
95-190	76.1a	0.217 mn	$0.4 \mathrm{m}$	3.1i-m	1.9d-f	1.7l-p	6
W-389 (94-127)	73.2a	0.245l-n	1.8lm	3.0j-m	0.2f	3.5b-g	14
W-388 (97-088)	72.1ab	0.200n	7.4 h-m	6.1e-m	0.4f	1.0o-q	19
95-102	72.0ab	0.184n	9.2g-l	8.9c-k	1.4ef	2.0j-o	8
95-161	71.9ab	0.182n	10.6g-k	9.2c-i	0.0f	1.9k-o	22
Sumor (W-201) (PI 566657) ^f	69.0ab	0.228nm	9.1g-l	4.8g-m	1.3ef	3.4c-h	26
Regal (W-152) (PI 566650) ^f	67.4a-c	0.355i-n	0.3m	0.9m	0.0f	2.6g-l	10
97-094	66.2a-d	0.271 j-n	7.5h-m	2.1k-m	1.2ef	3.0e-i	23
97-095	65.3a-e	0.261k-n	9.8g-l	5.7f-m	1.0ef	3.8b-e	19
White Regal	60.5b-f	0.333i-n	11.2f-k	4.2h-m	5.0b-f	2.6g-l	23
Tanzania (PI 595887) ^f	60.1b-f	0.224mn	8.3g-m	7.5d-m	0.0f	0.9pq	8
96-047	56.6c-g	0.467g-i	3.7k-m	5.5f-m	0.2f	2.9e-j	13
W-308	54.2d-h	0.510f-i	1.7lm	3.9h-m	0.0f	6.2a	11
Picadito (PI 634399) ^f	53.8e-h	0.420g-l	13.6d-i	9.1c-i	3.8c-f	2.7g-l	27
W-345	52.9f-h	0.458g-i	14.9d-h	5.8f-m	2.5c-f	2.0j-o	18
W-387 (98-294)	52.1f-i	0.421g-l	9.4g-l	11.3b-g	0.2f	5.7a	11
W-393 (95-233)	50.6f-j	0.433g-k	9.1g-l	7.4d-m	4.8b-f	2.2i-m	22
W-332	49.6f-j	0.450g-i	20.2b-e	10.0c-i	1.0ef	4.1b-d	26
95-175	49.6f-j	0.398h-m	13.0e-i	8.7c-k	1.4ef	3.7b-f	26
Liberty (W-341)	47.4g-k	0.414g-l	12.6e-j	12.7b-е	6.9b-f	3.5b-h	23
W-325	45.4g-k	0.575d-h	6.7h-m	14.2b-d	2.6c-f	6.4a	15
94-207	45.2g-k	0.666c-f	6.0i-m	5.2g-m	2.1d-f	2.8e-k	11
97-092	45.0g-k	0.593d-g	16.7d-g	5.5f-m	2.5c-f	4.5b	16
HiDry (W-190) (PI 566633) ^f	42.8h-l	0.781be	5.6i-m	14.4bc	g	2.8f-k	7
W-364	40.6i-l	0.546e-h	6.7h-m	4.6g-m	11.1b	3.3d-h	20
96-051	39.9j-m	0.689c-f	9.1g-l	9.0c-k	0.0f	2.1i-n	11
97-022	36.7k-m	0.736ed	13.0e-i	15.0bc	6.6b-f	2.7f-l	20
Tinian (PI 153655) ^f	36.5k-m	0.335i-n	28.6ab	17.1b	0.0f	0.6q	12
GA90-16 (PI 612703) ^f	32.3lm	0.395h-m	27.9a-c	31.8a	5.5b-f	1.1n-q	16
W-315	31.6lm	0.843bc	19.7c-f	8.1c-l	7.5b-e	6.1a	14
97-081	31.3lm	0.716с-е	21.8a-d	10.7b-h	8.7b-d	4.4bc	19
Beauregard (PI 566613) ^f	28.0m	0.948b	13.3e-i	12.2b-f	9.3bc	3.3d-h	19
SC1149-19 (PI 634401) ^f	8.4n	1.377a	30.1a	27.5a	27.8a	4.1b-d	22

Means within columns followed by a common letter are not significantly different (LSD; P = 0.05) (SAS Institute 1989).

siderably in these experiments; however, many of the USDA-ARS/Clemson University genotypes yielded as well or better than the commercial sweetpotato cultivars (Table 1). Only two of the experimental dryfleshed sweetpotato genotypes yielded significantly less than Picadito. These yield data must be viewed with caution, however, because soil type and relatively poor drainage at the USVL are not conducive to optimal sweetpotato production.

Twenty of the genotypes discussed in this article also were grown in Jamaica and evaluated for resistance to the sweetpotato leaf beetle, *Typophorus nigritus viridicyaneus* (Crotch), an occasional pest in the United States (Jackson et al. 2003). Several of these breeding lines exhibited significant levels of resistance to this pest, although most lines were not adapted well to the environment in Jamaica and did not produce as well as local cultivars.

Sweetpotato genotypes that are resistant to the sweetpotato weevil have been reported by researchers at the International Institute of Tropical Agriculture, The World Vegetable Center (AVRDC), National Agricultural Research Systems Institutes in South Asia, USDA-ARS, and universities in the United States (for review, see Smit 1997). However, most published reports on resistance to weevils have simply been screening of existing germplasm sources (Pillai and Kamalan 1977, Rolston et al. 1979, Hahn and Leuschner 1981, AVRDC 1987, Thompson et al. 1999). It was reported that not enough progress has been made to develop cultivars with stable resistance to sweetpotato weevil by using conventional breeding techniques (Collins et al. 1991). Talekar (1987) even concluded that an adequate source of resistance to sweetpotato weevil may not exist. However, we believe that useable levels of resistance to the sweet-

[&]quot;All sweetpotato genotypes (except Beauregard, Picadito, Tanzania, and Tinian) were from the USDA-ARS/Clemson University sweetpotato breeding program, USVL.

^b Wireworm, *Diabrotica*, and *Systena* (WDS) severity index: 1, 1–5 scars; 2, 6–10 scars; and 4, >10 scars, averaged over all roots; max score, 4.0.

 $^{^{}c}$ C. confinis.

^d Primarily P. aliena

^e C. formicarius elegantulus.

^f Plant Introduction number, National Plant Germplasm System, USDA-ARS, Griffin, GA (http://www.ars-grin.gov/cgi-bin/npgs/html/tax site acc.pl?S9%20Ipomoea%20batatas%20var.%20batatas).

g Not evaluated because of low infestation level.

potato weevil can be developed from existing germplasm sources by using conventional breeding techniques, if, as suggested by Smit (1997) and Collins et al. (1991), a systematic, multidisciplinary breeding approach with long-term support is followed. What is needed is an intensive recurrent breeding program that targets weevil resistance and uses the high selection pressure and precise evaluations such as those used by the USDA-ARS/Clemson University sweetpotato breeding program and demonstrated in the current study. Jones et al. (1976) showed that to make real progress in developing resistant cultivars, it is necessary to develop a dedicated polycross breeding program in which incremental progress in desirable characteristics, such as resistance to weevils, can be made (Cuthbert and Jones 1972). This has been done for other soil insect pests of sweetpotato, such as the WDS complex, wireworms, and grubs, for selection evaluations at the USVL (Cuthbert and Jones 1972). However, this has not been done for the sweetpotato weevil, due primarily to a lack of consistent high weevil pressure for selection evaluations at the USVL. Thompson et al. (1999) found that many of the plant introductions that were evaluated in Mississippi had resistance to both WDS and sweetpotato weevil. Thus, seems is possible to concurrently breed for resistance to both WDS and sweetpotato weevil. We suggest that useable levels of resistance in dry-flesh sweetpotato genotypes to several insect pests are achievable using a rigorous breeding approach with high selection pressure and precise evaluations of insect damage. Also, the determination and quantification of compounds responsible for antibiosis and antixenosis in sweetpotato germplasm would help accelerate this process.

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